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Fire, climate and vegetation linkages in the Bolivian Chiquitano Seasonally Dry Tropical Forest

M.J. Power¹, B. S. Whitney², F.E. Mayle³, D.M. Neves⁴, E. de Boer⁵, K. S. Maclean⁶

¹ Natural History Museum of Utah, Department of Geography, University of Utah, USA

² Department of Geography, Northumbria University Newcastle, Newcastle-Upon-Tyne, UK

³ Centre for Past Climate Change, Department of Geography & Environmental Science, University of Reading, Reading, UK

⁴ Royal Botanic Gardens, Kew, Richmond, UK

⁵ Faculty of Geosciences, Department of Geography, Utrecht University, NL

⁶ 2C Forthbridge Road, London, UK

ABSTRACT

South American seasonally-dry tropical forests (SDTF) are critically endangered, with only a small proportion of their original distribution remaining. This paper presents a 12,000 year reconstruction of climate change, fire and vegetation dynamics in the Bolivian Chiquitano SDTF, based upon pollen and charcoal analysis, to examine the resilience of this ecosystem to drought and fire. Our analysis demonstrates a complex relationship between climate, fire and floristic composition over multi-millennial time scales, and reveals that moisture variability is the dominant control upon community turnover in this ecosystem. Maximum drought during the early Holocene, consistent with regional drought reconstructions, correlates with a period of significant fire activity between 8,000 and 7,000 cal yr BP which resulted in a decrease in SDTF diversity. As fire activity declined, but severe regional droughts persisted through the mid-Holocene, SDTF, including *Anadenanthera* and *Astronium*, became firmly established in the Bolivian lowlands. The trend of decreasing fire activity during the last two millennia promotes the idea among forest ecologists that SDTF are threatened by fire. Our analysis shows that the Chiquitano seasonally dry biome has been more resilient to Holocene changes in climate and fire regime than previously assumed, but raises questions over whether this resilience will continue in the future under increased temperatures and drought coupled with a higher frequency anthropogenic fire regime.

Key words: fire, Chiquitano, Seasonally Dry Tropical Forest, climate, drought, Holocene

INTRODUCTION

Seasonally-dry tropical forests (SDTF) comprise over 40% of the world's tropical forested ecosystems, but they are afforded little protection, and have been extensively deforested over the past several centuries. Of the remaining SDTF, 16% occurs in South and Southeast Asia and 50% in Latin America (1). SDTF are limited to regions of the tropics that experience seasonal drought, occurring where annual rainfall is less than 1600 mm with a 5-6 month dry season (2). SDTF require fertile soils, hence they have been heavily cleared for agriculture over the past several centuries. Occurring under a similar climate, *cerrado* (upland) savannas differ from SDTF in that they are structurally open, containing abundant fire-tolerant woody species and a xerophilic herbaceous ground cover. Generally, *cerrado* (sensu stricto) savannas occur on less fertile soils compared to SDTF, but the boundary dynamics between SDTF and *cerrado*

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3 savannas are notoriously complex and have inspired many ecological studies to disentangle the
4
5 key drivers of forest-savanna ecotones (e.g. 3,4).
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9 Fire, whether natural or anthropogenic in origin, has long been recognized as a key
10 control upon fine-scale SDTF-savanna boundary dynamics over short-term ecological time
11 frames, but the relationship between fire and SDTF-savanna dynamics under high-amplitude
12 climate change predicted over the coming century is poorly understood and a key concern for
13 the conservation community, given the endangered status of both these ecosystems (5). The
14 lack of obvious plant-fire adaptations in a number of SDTF species has led many ecologists to
15 infer that this is not a fire-adapted biome, and that it is therefore highly vulnerable to burning (6),
16 a cause for concern in the future, as climate change is predicted to lead to increasing
17 temperatures and drought (7), which would no doubt lead to increased risk of fire.
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32 ***Fire and the Bolivian Chiquitano Seasonally Dry Tropical Forest (SDTF)***

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35 Our study area is the Bolivian Chiquitano SDTF – the largest intact, old-growth block of
36 SDTF in South America (1). This semi-deciduous to deciduous forest covers most of the
37 calcareous rolling hills of eastern Bolivia (Chiquitanía), interspersed with patches of upland
38 (*cerrado*) savanna where soils are either too nutrient poor or too thin to support forest (8).
39 These upland SDTF and *cerrado* savannas form an abrupt boundary at the Bolivia/Brazil border
40 with the seasonally-flooded savanna wetlands of the Pantanal basin, most of which lies in Brazil
41 to the east (Fig. 1). Fires occurring in the SDTF-*cerrado* savannah mosaics of Chiquitanía
42 today are primarily caused by humans clearing land for agricultural purposes. [The seasonally
43 wet and dry climate, with a June-October dry season, coupled with edaphic and hydrologic
44 controls on vegetation composition and structure, support large wildfires during the driest years,
45 when there is abundant dry biomass \(9\).](#)
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However, a serious cause for concern among tropical ecologists and conservation biologists is that anthropogenic fires are becoming increasingly common, not only burning in savannahs, but spreading into SDTF (10). This concern is predicated on the assumption by most ecologists that, unlike savannah, SDTF is not a fire-adapted ecosystem due to the lack of fire adaptation/tolerant features of many constituent arboreal species, and, in particular, the prevalence of fire-sensitive columnar cacti (*Cereus* spp.) in this ecosystem (6). However, the fact that some arboreal taxa (e.g., *Astronium* (*Myracrodruon*) *urundeuva* and *Aspidosperma quirandy*) have fire-resistant bark, raises the possibility of some degree of fire resilience within this ecosystem. The likelihood of local controlled fires escaping to become uncontrolled SDTF wildfires will only increase in the coming decades as forest flammability increases under a future warmer and drier climate (7), potentially posing a serious threat to the long-term viability of the SDTF ecosystem.

Tropical climate and fire linkages

The climate of the study area – the Chiquitania region of eastern Bolivia and the adjacent Brazilian Pantanal – experiences a highly seasonal climate whereby most of the annual precipitation falls during the austral summer (Dec-Feb) (Fig. 1). This precipitation comes from the South American Summer Monsoon (SASM) and is delivered to the study area via the South American Low Level Jet (SALLJ) (11). The study area has a six month dry season and average annual precipitation between 1700 and 1000 mm, which decreases from north to south (12). Mean annual temperature is ~ 25°C, but large changes in seasonal temperature have been recorded in the 20th century with highs greater than 40°C during the austral summer and low temperatures below 10°C during the austral winter (10).

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3 Modern climate-fire linkages in eastern Bolivia are influenced by both tropical Atlantic
4 and Pacific sea surface temperatures and moisture transport. Trade winds from the Atlantic
5 contribute to evapotranspiration as air masses move across the Amazon basin (13). The
6 development of strong convection (subsidence) over Amazonia provides a link to the tropical
7 Pacific via the east-west Walker circulation (14, 15), which results in large-scale redistribution of
8 seasonal moisture flux. The influence of climate variability on the Chiquitano seasonally dry
9 tropical forest (SDTF) is likely linked to changes in tropical Atlantic sea surface temperatures
10 that may have a strong influence on moisture variability and fire regimes in this area (16).
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21 INSERT FIGURE 1 (MAP)
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24 Considering a more Atlantic origin for drought and fire occurrence in Chiquitanía-
25 Pantanal may help explain changes in fire activity. Periods in the past decade, when above
26 average convective precipitation occurs over a warm tropical North Atlantic ocean, results in
27 subsidence to the south, over the Amazon and South Atlantic. The direct influence is a
28 displacement of Hadley circulation and northward migration of the ITCZ resulting in reduced
29 precipitation across the equatorial Atlantic and, subsequently, a reduction in moisture in western
30 and southern Amazonia (17), causing an intensified fire season (16). For example, during the
31 extreme drought of 2010, Chiquitanía-Pantanal experienced anomalously low precipitation and
32 extreme fire conditions that have been linked to reduced advection of Atlantic moisture into the
33 Amazon basin and the consequent failure of the low level jet to deliver moisture to the study
34 area (16) (Fig 1). These recent episodes of severe drought and fire could potentially cause rapid
35 alterations in the composition and structure of vegetation communities within the SDTF.
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54 ***Aims and Approach***

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3 Here, we use a palaeoecological approach, based upon the analysis of pollen and
4 charcoal from radiocarbon-dated lake sediments, to determine the long-term relationship
5 between fire, climate, and the Chiquitano SDTF over the Holocene period (the last 12,000
6 years). This multi-millennial time series spans intervals of time when the climate was
7 significantly drier than present (centred on the middle Holocene – 6,000 cal yr BP), thus serving
8 as a potential analogue (albeit imperfect) of vegetation-fire-climate linkages under future
9 increased drought predicted by most Global Climate Models (GCMs). This palaeoecological
10 approach therefore provides the necessary long-term perspective to assess the ecological
11 significance of SDTF responses to drought and fires observed by ecologists over recent
12 decades.
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26 The key aim of our study is to assess the response of the Chiquitano Dry Forest to long-
27 term fire activity and increased drought and thereby test the validity of the widely held
28 assumption that the SDTF is inherently susceptible to fire. If this hypothesis is correct, one
29 would predict that the Bolivian Chiquitano Dry Forest has a long-term history of low fire activity.
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38 **STUDY SITE AND METHODS**

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41 The study site, Laguna La Gaiba (-17.78°, -57.72°), is a large (55 km²), shallow (4-5 m
42 deep) 'over-flow' lake located along the course of the Paraguay River (Fig. 1) on the border
43 between Bolivia and Brazil. It lies along a fault line that defines the boundary between the
44 upland Chiquitano SDTF to the west and the seasonally-flooded [Pantanal wetlands to the east,](#)
45 [which includes both savannah and tree-less grasslands](#) (18). Seasonal rainfall over the
46 Pantanal basin and its river catchment causes widespread floods which drain into the Paraguay
47 River and its associated lakes. LLG is therefore closely linked hydrologically to the Pantanal
48 basin.
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3 This lake has yielded long-term palaeoclimate records, inferred from reconstructed lake
4 level changes (19-21) and pollen-based vegetation reconstructions (22, 23). These records
5 indicate that eastern Chiquitanía and the Pantanal have undergone significant changes in
6 hydrology, climate, and biome turnover since the Last Glacial Maximum (LGM). Laguna La
7 Gaiba is surrounded by a mosaic of plant communities, the distribution of which is dependent on
8 local topography, edaphic conditions, and hydrology. The lowest elevation areas, such as those
9 adjacent to the northeastern boundary of LLG along the Paraguay River, support extensive
10 flooded wetland savannah. Seasonally-inundated savannas occur to the east of the main trunk
11 of the river and support mosaics of seasonally-dry tropical forests on local areas of higher
12 terrain, such as ancient river levees. In the immediate vicinity of LLG, the steep slopes of the
13 Amolar Hills, rising up to 600m above the influence of seasonal flooding, form the eastern
14 margin of the Chiquitano SDTF (10). Deciduousness of the SDTF increases with elevation and
15 open canopy scrub vegetation and *cerrado* savanna occur on the summit of the hills, where
16 soils are too thin to support forest (8).
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34 Previously published pollen abundance and richness data, together with limnological
35 data, from LLG (21-23) are compared with a high-resolution charcoal record from the same core
36 to enable the relationship between the Chiquitano SDTF, climate and fire, over the entire
37 Holocene, to be explored for the first time. The LLG record extends beyond 40,000 yrs BP and
38 demonstrates large-scale landscape rearrangement and catchment change in the western
39 Pantanal at the end of the Pleistocene (21, 22). Our analysis focuses on the last 12,000 years; a
40 period defined by landscape stability, the establishment of modern lake conditions, and the
41 spread of SDTF in eastern Chiquitanía (22-23).
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52 The fire history reconstruction from LLG was accomplished by analyzing macroscopic
53 (>125µm) sedimentary charcoal at contiguous 0.5 and 1-cm intervals throughout the entire
54 sediment core (see 24) and analyzed using the chronology of Whitney *et al.* (22). [Charcoal](#)
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3 analysis for each sediment sample was completed by placing the sample in a 15 ml tube in a
4 hot water bath of 10% potassium hydroxide solution for 15 minutes and then gently washed
5 through a 125 μm screen. All remaining residues were examined at 36X magnification and all
6 charcoal particles greater than 125 μm were tallied. Charcoal counts were then converted to
7 concentration (particles cm^{-3}) and charcoal accumulation rates (CHAR, particles $\text{cm}^{-2} \text{yr}^{-1}$).
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15 The CHAR record was then decomposed into two components, a low frequency
16 background trend and a high-frequency peaks component, referred to as fire episodes.
17 Background charcoal (BCHAR) captures the slowly varying trends in CHAR through time as
18 vegetation composition and structure changes, while the peaks component aids in the
19 identification of one or more fire events (25). At LLG, BCHAR was summarized using a Lowess
20 smoother that is robust to outliers with a 300-year window width. Peak detection in the charcoal
21 record was tested for significance using a Gaussian distribution and only those peak values
22 exceeding the 95th percentile were considered significant (26). Once fire events were identified,
23 all charcoal peaks were further screened to eliminate those peaks resulting from statistically
24 insignificant variations or noise in CHAR (27). Three metrics of fire activity are considered from
25 the LLG charcoal record: CHAR or changing influx of charcoal through time, fire-episode
26 frequency, expressed as number of fires episodes or "peaks" in charcoal production per 1000
27 years, and peak magnitude, a measure of the total amount of charcoal associated with each
28 peak, which is likely related to the fire size, intensity and charcoal delivery to the lake.
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46 To explore possible fire-climate-vegetation drivers at LLG through time we obtained the relative
47 contribution of fire and precipitation proxies in explaining temporal variation in community
48 composition of SDTF (16 taxa), savannahs (12 taxa) and riparian forests (21 taxa) by following
49 methods similar to those proposed by Legendre *et al.* (28). Because these three plant
50 communities (SDTF, savannahs and riparian forests) are distributed across distinct edaphic
51 conditions (eutrophic, dystrophic and seasonally flooded soils, respectively), with few or no
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3 overlap in species composition, the variation partitioning analyses were performed separately
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5 for each one of them. We tested the overall significance of the fire fraction (controlled for
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7 variation in moisture) and the moisture fraction (controlled for variation in fire) by applying a
8
9 permutation test (999 permutations) for redundant analysis. All proxy datasets used for the
10
11 variation partitioning analyses were pre-smoothed to have the same temporal resolution, and
12
13 comprise (i) macroscopic charcoal influx data (this paper), (ii) algal community change,
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15 interpreted to be controlled by precipitation-driven lake level change (first axis of principal
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17 components analysis in reference 19), and (iii) relative pollen percent abundance data, which
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19 have been assigned to categories reflecting each of the three main vegetation community
20
21 categories around Laguna La Gaiba (22, 23) (Table I). Even though the temporal resolution
22
23 applied here make it challenging to address the role of fire and flooding on short-term ecological
24
25 processes driving community turnover, recent studies have shown woody vegetation is shaped
26
27 by regularly occurring floods and fires (9, 29). All variation partitioning analyses were conducted
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29 using the vegan (30) package in the R Statistical Environment (31).
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34 INSERT TABLE 1
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36 RESULTS AND INTERPRETATION 37 38

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40 Partitioning the variation explained by the environmental predictors revealed that
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42 precipitation (*Pediastrum algae*) and fire-related (charcoal) proxies explain 27% and 2%,
43
44 respectively, of the turnover in community composition in savannah ecosystems. In addition, 2%
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46 of the turnover in savannahs is a shared component between precipitation- and fire-related
47
48 proxies. In the riparian forests, precipitation- and fire-related proxies explain 18% and 2%,
49
50 respectively, of the turnover in community composition, while the precipitation-related proxy is
51
52 the sole factor explaining turnover in SDTF composition (27%). Furthermore, 69%, 80% and
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54 73% of the turnover in savannahs, riparian forests and SDTFs, respectively, remains
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56 unexplained (Fig. 2).
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INSERT FIGURE 2

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9 Most of the turnover in community composition that we are able to explain is assigned to
10 the precipitation-related proxy. However, the fire-related proxy or CHAR showed a weak, but still
11 important, signature in the turnover of savannahs. The clear fire adaptations of savannah plants
12 - such as thick, corky bark; the ability to root-sprout from substantial rhizomes; and protected
13 buds - demonstrate that fire has been a key ecological force in savannah (32-34). Because
14 these adaptations appear to be either lacking or have received minimal research attention in
15 present-day SDTF, ecologists have hypothesised that fire was not a strong ecological force in
16 this biome (6). Furthermore, even though the precipitation-related proxy explains most of the
17 turnover in riparian communities, the fire-related proxy also showed a signature in the turnover
18 of these communities. The ecological role of fire in SDTF, growing primarily to the west of LLG
19 today, in the Chiquitanía region of eastern Bolivia, remains uncertain due to the paucity of
20 suitable palaeo archives (lake and bog sediments) in this landscape. North and east of LLG are
21 the Pantanal tropical wetlands, which are a mosaic landscape dominated by seasonally-flooded
22 savannahs and riparian gallery forests and shaped by regularly occurring floods and occasional
23 wildfires (9, 18, 35).

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42 The relative contribution of charcoal from different neighbouring ecosystems –
43 savannah, riparian communities, and SDTF – to the sediments of LLG is difficult to establish.
44 However, because the preponderance of pollen deposited in LLG originates from upland
45 Chiquitano SDTF to the west of LLG (22, 23), it is likely that most of the charcoal entering this
46 lake similarly originates from the Chiquitano SDTF, rather than the Pantanal wetlands to the
47 east. Furthermore, the lack of correlation between sediment particle size and charcoal
48 abundance supports our inference that most of the charcoal entering LLG is aeolian in origin,
49 rather than entering the lake via erosion from the surrounding slopes or pulses of fluvial input
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3 from the Pantanal wetlands. It seems likely that, under extreme drought conditions of the middle
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5 Holocene, fires occurring in the savannah and riparian communities of the Pantanal would have
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7 penetrated into the eastern Chiquitano SDTF.
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10 While the environmental component (precipitation and fire) is relatively straightforward to
11 interpret, there remains a large fraction of turnover in community composition that is
12 unexplained (69%, 80% and 73% of the turnover in savannahs, riparian forests, and SDTFs,
13 respectively) in the LLG record. There are many factors potentially important to determining the
14 community composition of assemblages that we have not adequately accounted for, such as: 1)
15 ecological drift (c.f. 36) driving stochastic rearrangements of species distribution ranges through
16 time; 2) biotic processes that were not measurable (e.g. competition, natural enemies); 3)
17 environmental factors that were not measured and uncertainties inherent to the proxy
18 measurements (Table I). Despite these factors, such a high proportion of unexplained variation,
19 ranging from about 33% to 75% (e.g. 37-39), is a common outcome in studies of floristic
20 turnover.
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38 The partitioning analysis shows that drought influences SDTF community composition
39 and our pollen data show that closed-canopy forest remained throughout the Holocene with no
40 evidence of increased savannah-type vegetation until recently (Fig. 3), which would be expected
41 if the forest was replaced by an open-structure vegetation. The period of Holocene drought,
42 identified from high abundance of shallow-water indicators (*Pediastrum argentinense* algae)
43 from 10,000 to 4,400 cal yr BP (19), corresponds with compositional change shown by
44 increases in the key dry forest taxon *Astronium* and a reduction in Moraceae (Fig. 4d and 4b),
45 which is more prevalent in pollen assemblages from wetter climates (40, 41). Fire activity, or
46 CHAR, however, does not correlate with these changes in forest composition (Fig. 3). Fire
47 frequency is highest during the Holocene transition, 12,000 cal yr BP, but then low CHAR
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3 values during the early Holocene (10,000 cal yr BP) (comparable to those of today) increase to
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5 maximum values by 7,500 cal yr BP. Extreme fire activity by 7,500 cal yr BP lags behind the
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7 beginning of early Holocene drought at Botuvera Cave (42) and changes in SDTF composition
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9 at La Gaiba by approximately two millennia (Fig.5b), supporting the results of our partitioning
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11 analysis that shows drought, not fire, to be the key influence on SDTF vegetation turnover.

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14 Although increasing CHAR values by 7,500 cal yr BP do not significantly change the abundance
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16 of the key SDTF taxa, thus not leaving a signature in the SDTF community turnover, the
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18 increased fire pressure causes a decline in vegetation richness captured by LLG pollen richness
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20 index (Fig. 4a). Therefore, the combined effects of drought and fire negatively impacted plant
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22 diversity of the eastern Chiquitano SDTF as more drought-tolerant taxa (*Astronium* and
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24 *Anadenanthera*) increased in relative abundance.
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28 INSERT FIGURE 4
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31 The floristic composition of the SDTF subsequently altered towards a more moisture-
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33 dependent forest community in the late Holocene (e.g. expansion of Moraceae) as precipitation
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35 increased once more, resembling the modern forest composition by 3,000 cal yr BP. This
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37 compositional change was driven by rising precipitation, beginning 4,400 cal yr BP at La Gaiba
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39 (19), and corroborated by a number of lake records across the region (43, 44). Floristic changes
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41 lagged behind the reduction in fire activity by several millennia. There were no discernible
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43 variations in the pollen record concomitant with lower fire activity after 6,000 cal yr BP when
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45 CHAR sharply declined (Figs. 3 and 4c). Again, this temporal mismatch between peak fire
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47 activity and precipitation-driven compositional changes confirms our partitioning analysis which
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49 indicates fire is important, but not the key driver of SDTF community turnover (Fig. 2).
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52 53 DISCUSSION

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56 *Influences of past fire and climate on SDTF*
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3 The charcoal record from La Gaiba indicates that fire was a persistent feature in eastern
4 Chiquitano SDTF, with periods of intensive fire activity during extended droughts. Despite the
5 clear role of drought and fire in the development of the Chiquitano SDTF over the Holocene,
6 there is a complex relationship at play among precipitation, floristic composition, and fire at the
7 boundary with the Pantanal. Lower precipitation, and hence reduced flooding compared to
8 present, in the early to mid-Holocene would have resulted in greater coverage of ignitable, dry
9 savanna areas in the Pantanal, because the seasonal inundation of the basin and length of
10 flood season is highly dependent on the strength of the SASM delivered to the region through
11 the SALLJ. Palaeo-precipitation reconstructions from speleothem $\delta^{18}\text{O}$ records ~1500 km
12 southeast of LLG (downstream in the path of the SALLJ) capture the centennial-to-millennial
13 scale droughts during the early to middle Holocene (Fig. 5a and 5b) that have been linked to
14 changes in the strength of the SASM (42, 45). Modern precipitation-hydrological studies have
15 demonstrated a strong link between annual rainfall over the Pantanal and the extent and length
16 of flooding over the last century (12). Furthermore, historical periods of extended drought across
17 the Pantanal reduced seasonally-inundated landscapes and vegetation types (12).

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Drying across the Pantanal basin in the early to mid-Holocene is demonstrated by the proxy data from La Gaiba (19, 20), but also corroborated by several records influenced by the path of the SALLJ. These include L. Titicaca, which progressively decreased in lake level beginning ~ 7,500 cal yr BP (44), and the Lapa Grande Cave record (45), [which reports several large amplitude dry climate anomalies, persisting for several centuries, centred at 7,800 and 7,400 cal yr BP \(Fig 5a\). Similar century-long droughts occur at Botuvera Cave, located at 27°S, near the exit of the SALLJ, demonstrating the regional impact of drought conditions during the early Holocene \(Fig 5b\). Although stable oxygen isotope profiles differ at times in the Holocene from the LLG CHAR record, there are provocative linkages among these proxies at multi-centennial and millennial-scales.](#) For example, centuries of reduced flooding in the

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3 Pantanal during extreme drought centred at 7,800 cal yr BP would have limited inundation in
4 savannahs, creating optimal conditions for frequent fire ignition in these highly flammable grass-
5 dominated systems. Our partitioning analysis supports this interpretation, as fire and drought
6 are both shown to contribute to a considerable fraction of the variation in savannah community
7 (Fig. 2).
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15 This higher fire activity raging across the Pantanal basin during the mid-Holocene period
16 of intense drought likely penetrated the SDTF of the eastern Chiquitano region, spreading
17 through the undergrowth, as pollen representative of key SDTF understorey taxa, such as
18 *Clavija* and *Sapium*, are removed from the rich diversity of taxa (see 23). Interestingly, pollen of
19 *Cereus* columnar cactus, one of the key SDTF taxa used to argue for the fire intolerance of
20 SDTF (5), is present during periods of higher fire activity around 8,500 and again at 1,500 cal yr
21 BP (Fig 4b and 4c). Its presence may reflect a high degree of spatial variability and/or
22 decreased fire frequency in the eastern Chiquitano SDTF during the early Holocene and again
23 in the late Holocene. Its survival in fire-influenced SDTF may reflect its dispersal capability
24 across the catchment, possibly favouring rocky areas with little ignitable ground cover, allowing
25 small populations to persist (today *Cereus* spp. are common components of the forest around
26 La Gaiba). Despite the inferred changes to the plant diversity and potential impacts of fire on the
27 understorey composition [as well as on the low abundance taxa of the eastern Chiquitano SDTF](#)
28 [during the mid-Holocene \(e.g. temporary exclusion of *Tabebuia* and *Phyllostylon*\)](#), the dominant
29 tree taxa of the dry forest (e.g. *Astronium* and *Anadenanthera*) were not replaced throughout the
30 period of intensive fire activity (Fig. 4d), implying that SDTF is at least partially resistant to the
31 fires originating in the Pantanal.
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51 *Fire and Conservation in SDTF* 52 53 54 55 56 57 58 59 60

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Fire has been a persistent feature in the eastern Chiquitano SDTF, thus refuting our hypothesis that fire has played no role in shaping the diversity patterns in the Chiquitano SDTF (e.g. 6). The recent decline in fire activity during the last two millennia might have fuelled the perception that fires have had a limited role in the evolution of SDTF. Critically, the floristic composition and diversity observed today in the eastern Chiquitano SDTF is a direct result of the palaeoclimate history, which in turn, had a strong influence on its history of varying fire activity. As suggested by Colinvaux (46), the high species richness across Amazonia is driven by the extensive land area, a wide range of habitats, as well as intermediate levels of natural disturbance, including both floods and fires.

Recent intense drought events have contributed to reductions in rainfall and soil moisture and increasing air temperatures, such as during the widespread droughts and fires of 2005 and 2010 (16, 47). Future management of fire-vegetation dynamics in the SDTF requires knowledge of natural variability on short and long time scales and consideration of how those processes link climate change to impacts on biological diversity (e.g. 48). The maintenance of closed-canopy SDTF during periods of increased fire activity during the early Holocene may serve as an ecological analogue for future conditions, as drought intensity and fire frequency are expected to continue increasing (7). The Chiquitano SDTF, and neighbouring dry forest corridor (49), however, may not be representative of all SDTF systems, as they have a very different flora and history compared to the endemics-rich, isolated SDTF of the inter-Andean valleys. These unique and isolated SDTF of the inter-Andean valleys have experienced a separate evolutionary history to lowland SDTF, having been separated for ca. 10 Myr (50). Andean SDTF may very likely show a sensitivity to fire that is not demonstrated by the lower diversity Chiquitano forest taxa which have shown resilience and adaptability in occupying new regions through rapid post-glacial migration (23,51). Regardless of whether inter-Andean valleys dry forests would be able to maintain a closed-canopy structure in the event of high fire activity,

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3 they contain some of the highest concentrations of endemics in the world (52), and the negative
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5 impact of fires on plant richness could have a devastating effect on these biodiversity hotspots.
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9 Our palaeoecological data show that the eastern Chiquitano SDTF withstood periods of
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11 intense droughts combined with increased fire activity during the Holocene (challenging the
12
13 widely held view of susceptibility of SDTF to fire), but the combined effects of these pressures
14
15 will be exacerbated in the future, with more frequent fires of anthropogenic origin, in addition to
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17 the projected increase in drought frequency/severity and warming in the region (7). Not only is
18
19 the Chiquitano SDTF under increasing agricultural pressures, but the neighbouring Pantanal
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21 savannas have been experiencing intensifying cattle ranching activities, which includes heavy
22
23 use of fire and invasion of fire-tolerant grass species (10). The Chiquitano SDTF could very
24
25 likely get caught in a 'squeeze' from escaped fires from both systems, which alongside
26
27 increasing fragmentation and drought, could cause irreversible changes to the vegetation,
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29 opening the canopy and allowing for elevated fire frequency to persist in the system. The future
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31 of SDTF ecosystems depends partly on their inherent ability to survive fire impacts.
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45
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53
54 improving this manuscript.
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18 19 FIGURE AND TABLE CAPTIONS

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23 Figure 1: Regional map of tropical South America, lower right inset shows the location of
24 Laguna La Gaiba and vegetation communities around the research site, including the
25 seasonally dry tropical forest (SDTF), cerrado savanna, Dry Chaco, inundated tolerant forest,
26 palm swamps, and the seasonally flooded Pantanal. The coring site location is marked with an
27 'x' and occurs in the deepest portion (>5 m) of the lake. Inset climograph from Cuiaba, Brazil,
28 approximately 250 km northeast of Laguna La Gaiba, showing the seasonal timing and length of
29 dry season, May to September, based on 1981-2000 climatology (gray). Red histograms and
30 line plot show precipitation and temperature values during 2010 at LLG from gridded CRU TS
31 3.22 climate data.
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36 Figure 2: Variation partitioning by redundant analysis to determine how much of the temporal
37 variation in floristic composition in Laguna La Gaiba was accounted for by the environmental
38 variables measured (charcoal, pollen and *Pediastrum* proxies). Black fraction represents the
39 precipitation component (controlled for variation in fire), light grey fraction represents the overlap
40 between precipitation and fire components, and dark grey fraction represents the fire
41 component (controlled for variation in precipitation). Variation partitioning among other
42 paleoclimate proxies (e.g. $\delta^{18}\text{O}$ speleothem records from 42 and 45) and LLG charcoal and
43 pollen data was explored, but results were insignificant and are not shown.
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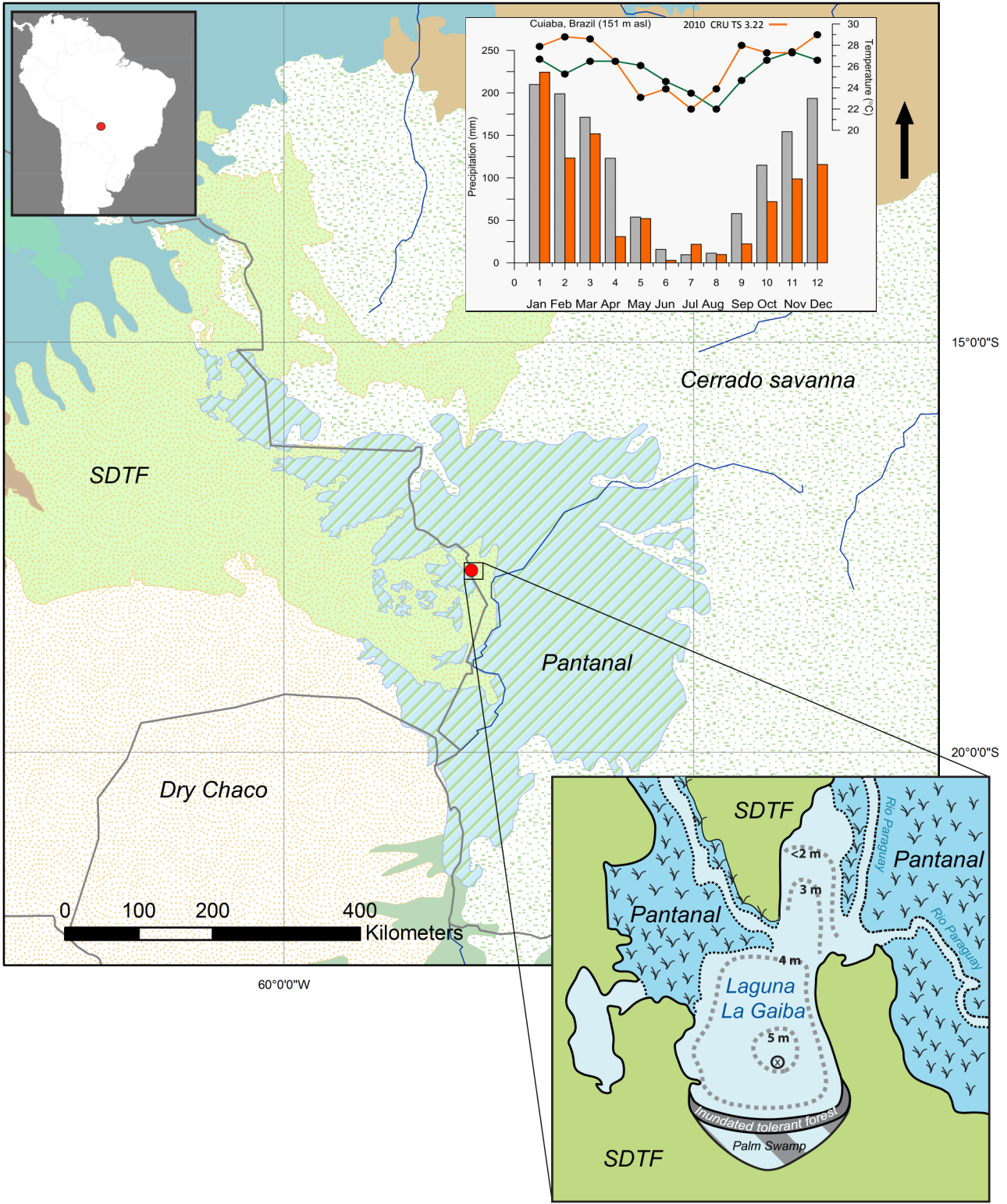
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47 Figure 3: Laguna La Gaiba charcoal influx (CHAR or particles $\text{cm}^{-2} \text{yr}^{-1}$) with lowess smoother
48 showing background charcoal (black line), fire episodes (top red vertical bars) as identified by a
49 300-year background window and local threshold (see 26). Pollen-based biome summaries (22)
50 for SDTF-type (green), savannah-type (yellow) (which may include aquatic grasses), and
51 riparian forest-type (blue) are presented as in Metcalfe et al (21). The percentage of all other
52 pollen types not contributing to these three community types including; *Poaceae*, (averaging
53 46%) and *Cyperaceae* (averaging 16%) for the Holocene is shown in gray. Particle size
54 analysis shows the clay (4-62 μm) and sand (125-1250 μm) fractions, *Pediastrum argentinense*
55 is shown as an indicator of shallow water conditions (19), and fire frequency (red) is expressed
56 as the number of fire episodes per 1000 years. Lastly, fire episode magnitude (shown at bottom
57 as a red histogram) represents the amount of CHAR exceeding average background CHAR with
58 each fire episode.
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3 Figure 4: A) vegetation richness, determined with rarefaction analysis of pollen data (53), B)
4 percent Moraceae and Cactaceae pollen C) charcoal influx and D) percent *Anadenanthera* and
5 *Astronium* pollen. All pollen percentage data are based on total terrestrial pollen sum (22).
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10 Figure 5: LLG transformed charcoal influx using the box-cox transformation (54) is compared
11 with three paleo-precipitation proxies. A) the $\delta^{18}\text{O}$ speleothem record from Lapa Grande Cave,
12 Brazil (-27.21° lat, -49.15° lon) (45), B) the $\delta^{18}\text{O}$ speleothem record from Botuvera Cave, Brazil
13 (-14.42° lat, -44.36° lon) (42), and C) lake level reconstruction from two sediment cores, C90m
14 and C150m, from Lake Titicaca. $\delta^{13}\text{C}$ records were used from Lake Titicaca sediments to
15 develop transfer functions to infer past changes in lake level (44).
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19 Table I. Summary of the environmental proxy data used for the partitioning analysis, the
20 interpretation of the proxy measurements, and sources of uncertainty in the environmental
21 reconstructions
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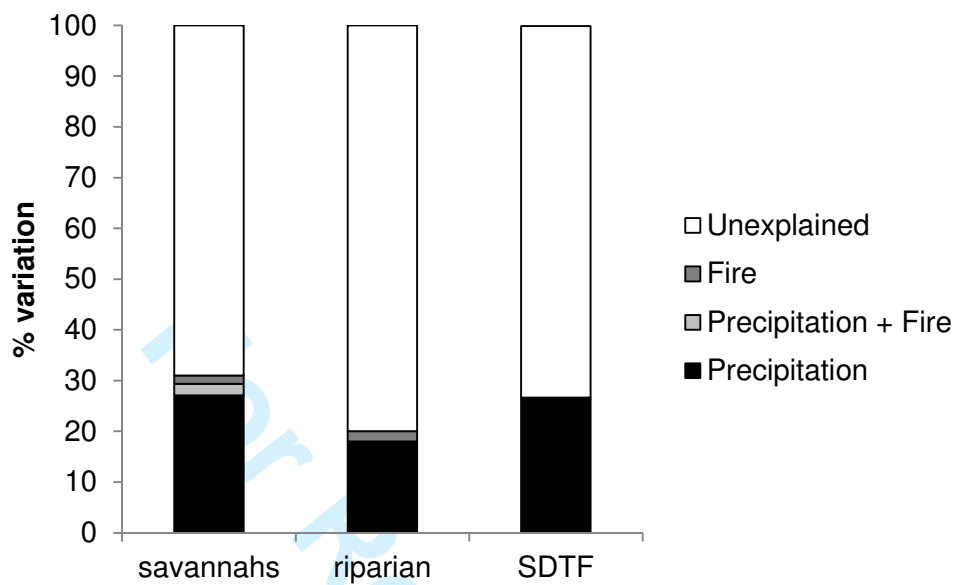
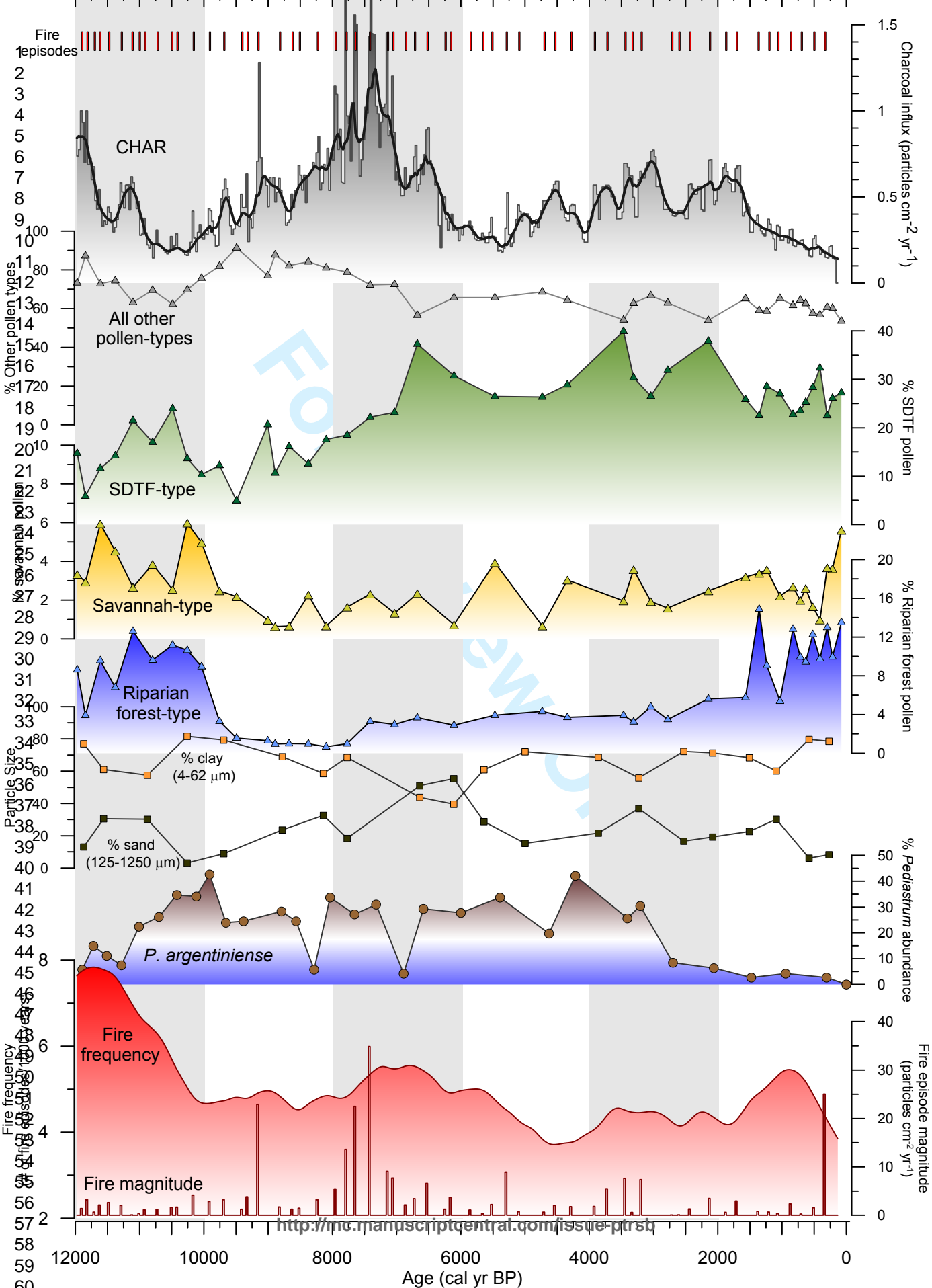


Figure 2



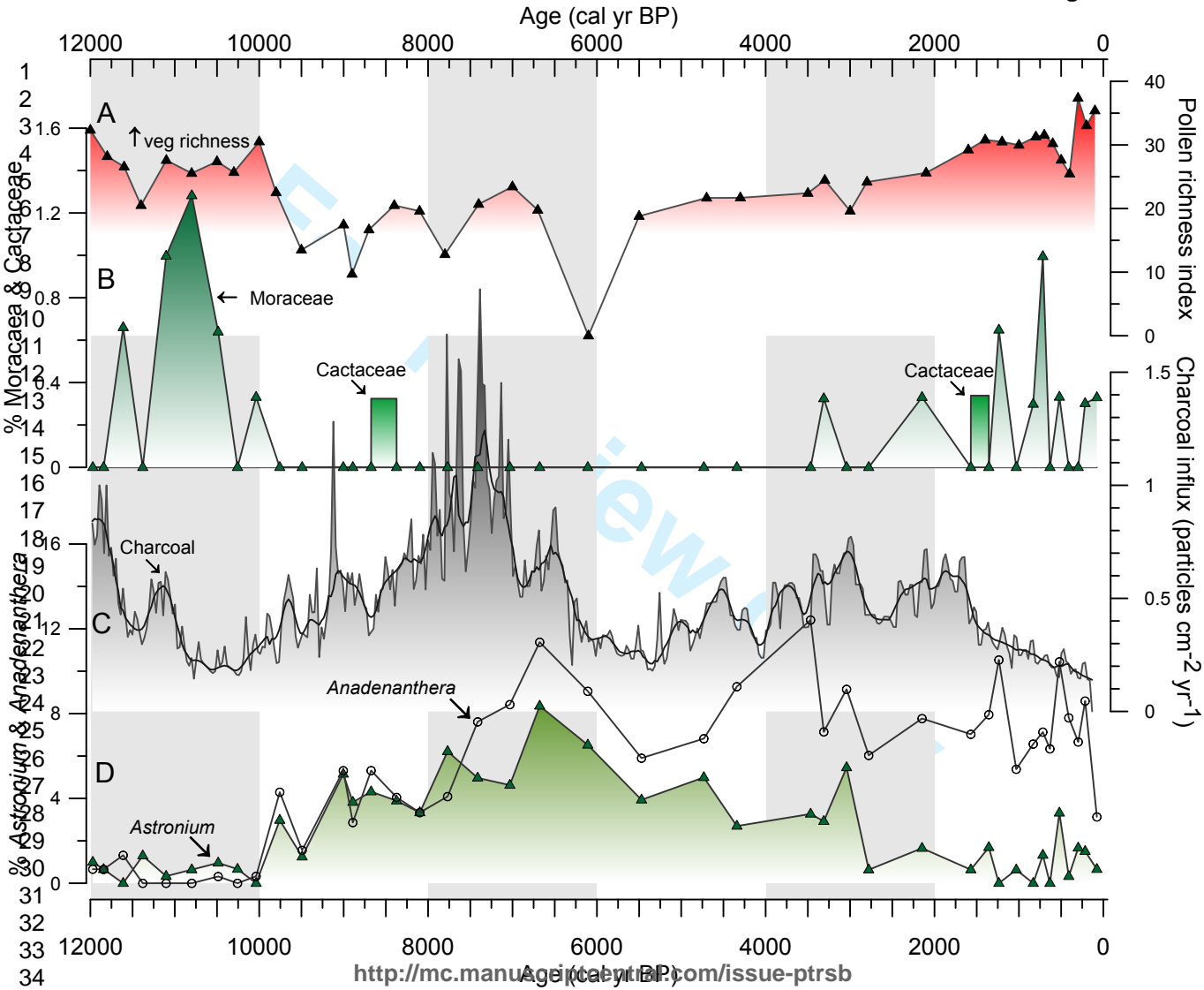


Fig 4.

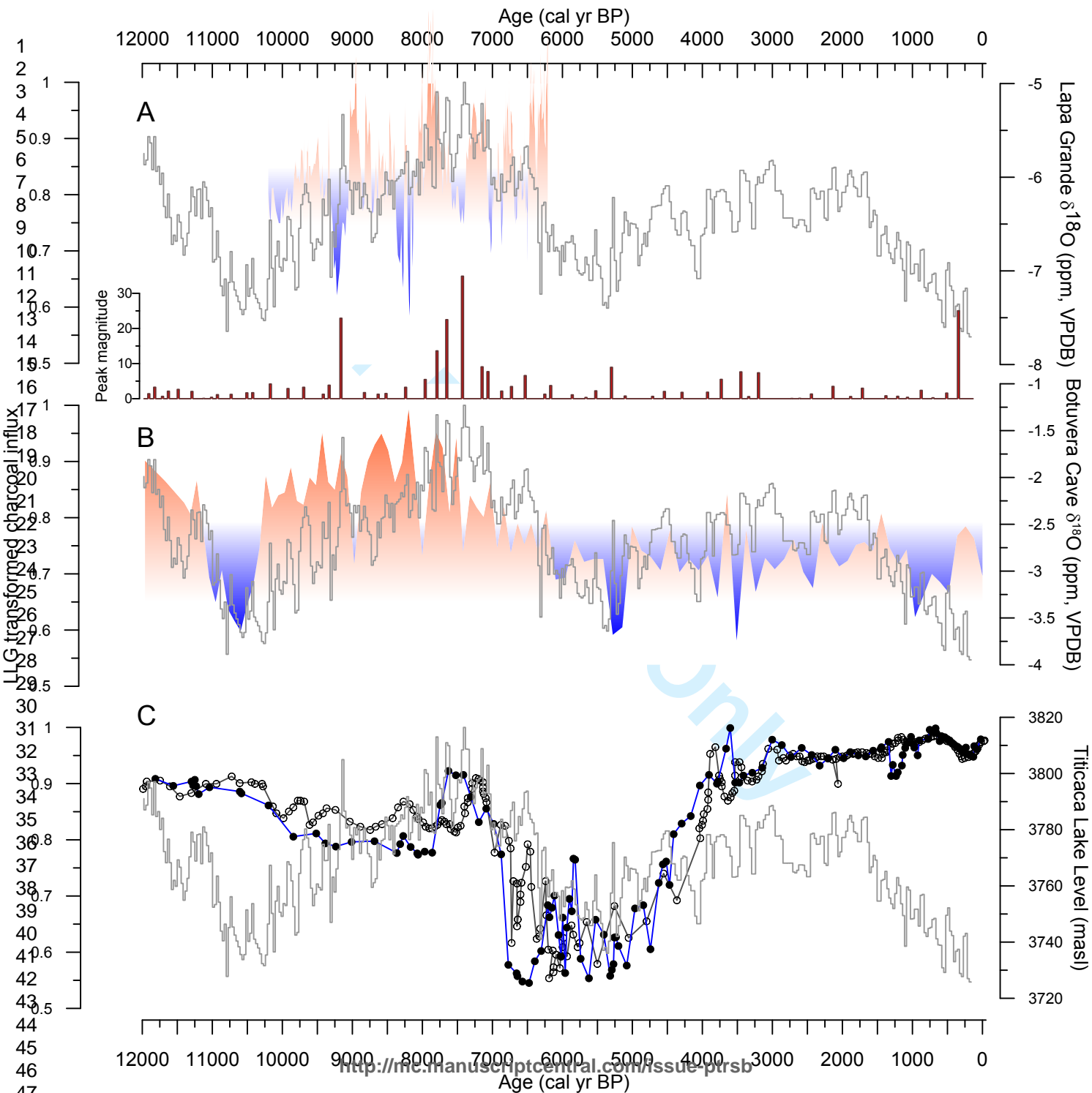


Fig.5

Table 1

Environmental variable	Proxy measurement	Proxy interpretation	Sources of uncertainty	Data Reference
Fire Activity	Macroscopic charcoal (> 125 μm) influx	Past local fire activity is proportional to charcoal influx	Errors in age-model of sediment accumulation	This paper
Vegetation	Relative percent pollen abundance	Variations in pollen types reflect community change in surrounding vegetation	Not all pollen types can be assigned to a single vegetation category Spatial & temporal variations in relative influence of wind- vs. flood-transported pollen	Whitney et al., 2011; 2014
Precipitation	<i>Pediastrum</i> community change	Variations in proportion of algal types restricted to shallow water is controlled by lake level change; driven by regional precipitation	Variation in influences of evaporation, local hydrology and precipitation on lake levels Organisms to respond to multiple interacting environmental variables	Whitney & Mayle 2012